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# Deep-sea fish assemblages (300–2100 m) in the eastern Pacific off northern Mexico

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ABSTRACT: Effective management of potential fisheries in deep-sea environments (>200 m depth) requires better understanding of species distributions and related environmental factors. We described the bathydemersal fish assemblages (300-2100 m) off the western coast of Baja California, Mexico (23–32°N) and their relationship with latitude, depth, temperature, dissolved oxygen (DO), salinity, organic matter, sediment composition and organic carbon. We collected a total of 3417 fish using a benthic sledge (18 orders, 36 families and 77 species: 27 mesopelagic, 10 bathypelagic and 40 bathydemersal; 8 new records). We found 5 latitude-depth assemblages: South-Shallow (<28°N, <700 m), South-Medium (<28°N, 700-1300 m), South-Deep (<28°N, 1430 m), North-Medium (>28°N, 700-1300 m) and North-Deep (>28°N, 1300-2100 m). Tropical species dominated southern assemblages, whereas northern assemblages shared species with the Southern California assemblages. A reduced number of bathydemersal species (15 species) dominated the upper slope. The middle slope (27 species) was the most diverse stratum, and lower abundances generally characterized the lower slope (12 species). Depth, DO and different water masses affected the distribution of bathydemersal species. These results are consistent with slope assemblages from different ocean basins, supporting the hypothesis that slope fish assemblages generally occupy discrete vertical ranges determined by depth and the environmental factors associated with it.

KEY WORDS: Bathydemersal fish · Environmental factors · Oxygen minimum zone · Southern Californian Pacific ecoregion · Salinity · Slope zonation · Latitudinal transition · Tropical species

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# **INTRODUCTION**

Effective management of potential fisheries in deep-sea environments (>200 m) requires better understanding of species distributions and related environmental parameters (Paramo et al. 2012, Anderson et al. 2013, Cunha et al. 2017). Assemblages vary mainly in relation to latitude, dissolved oxygen concentration (DO), substrate type, basin morphology, the presence of physical barriers and water masses with different physicochemical conditions, mainly temperature and salinity (Hamukuaya et al. 2001, Levin 2003, Fossen et al. 2008). The reduced concentration of DO (< $0.5 \text{ ml } l^{-1}$ , between 200 and 1000 m, generally) in oxygen minimum zones (OMZs) limits the vertical distribution of species and acts as a physiological barrier, especially for benthic species (Levin 2003, Gallo & Levin 2016). The major OMZs occur along the Eastern Pacific, off West Africa, in the Arabian Sea and in the Bay of Bengal (Levin 2003, Banse et al. 2014). Many species occur within more or less established depth intervals above or below the OMZ. However, some species inhabit the OMZ or undertake



Fig. 1. Study area and sampling stations of deep-sea fishes off the west coast of Baja California (BC), Mexico (NBC: northern BC, SBC: southern BC).
(•) TALUD XV research cruise (2012); (•) TALUD XVI (2013); (•) TALUD XVI-B (2014)

vertical migration (Wishner et al. 1995, Tolimieri & Levin 2006, Tolimieri 2007).

At local and regional scales, diversity in the deepsea is generally patchy (Jumars 1976, Gage & Tyler 1991) and is influenced by local environmental conditions. Many diversity 'hotspots' occur in high productivity environments (Tolimieri et al. 2015), such as hydrothermal vents, submarine mountains and canyons (Gage & Tyler 1991, Fossen et al. 2008, De Leo et al. 2010). The structure of marine faunal assemblages often relates strongly to water masses and depth, with depth likely acting as a proxy for other factors like pressure or DO (Powell et al. 2003, Tolimieri & Levin 2006, Anderson et al. 2013, Papiol et al. 2017). Studies on faunal assemblages of the continental slope elsewhere recognized 3 main depth zones: (1) upper slope (~300–600 m), (2) middle slope (~800– 1300 m) and (3) lower slope (~>1300 m) (Haedrich & Merrett 1988, Zintzen et al. 2012 and references therein), determined by local topography (Mediterranean Sea; D'Onghia et al. 2004), strong OMZ presence (Eastern Pacific; Tolimieri & Levin 2006, Tolimieri 2007, Anderson et al. 2013, De Leo et al. 2017), distinct water masses, as seen in several regions from the Atlantic Ocean (e.g. Powell et al. 2003, Menezes et al. 2006, 2009, 2015) or by the combined effect of water masses and DO concentrations (Southeastern Atlantic; Hamukuaya et al. 2001). The specific depth ranges vary regionally with oceanographic conditions (Ross et al. 2015, Quattrini et al. 2017).

The western coast of Baja California (BC) is located in the eastern Pacific off the Baja California Peninsula, Mexico (between 22 and 32° N; Fig. 1), within the Southern Californian Pacific ecoregion (SCP) (Wilkinson et al. 2009). The SCP begins at the southern tip of BC (22° 50' N), and extends along the Pacific coast to the north of Punta Conception, California, USA (34° 30' N). The California Current (0-300 m; low temperature, low salinity and high DO) provides temperate water from the North Pacific to the SCP and covers almost all of BC during the winter (Lynn & Simpson 1987). The California Undercurrent and the North-Equatorial Current (200-500 m; warm, high salinity and low DO) provide subsurface waters from the south, reaching as far as Southern California (34° N) during the summer (Lynn & Simpson 1987, Nam et al. 2015, Papiol et al. 2017).

During the summer, tropical and temperate water masses influence the BC continental slope. During our cruises, Papiol et al. (2017) recorded North Pacific Intermediate Water (NPIW; depth: ~200–1000 m, salinity: <34.5, temperature: ~5–8°C) off the northern part of BC (NBC: 28–32° N) and Equatorial Subsurface Water (ESsW; depth: ~200–500 m, salinity: 34.4–35, temperature: 8–15°C) off the southern part of BC (SBC; 23–27° N) and Pacific Deep Water along the entire BC (PDW; depth >1000 m, salinity >34.5, temperature <4°C). Pacific Intermediate Water (PIW; depth: 500–1200 m, salinity: 34.5–34.8, temperature: 4–9°C), widely distributed in the Eastern Central Pacific (ECP), was also recorded in SBC (Pantoja et al. 2012).

In contrast to similar OMZs in SBC and ECP (75-1200 m deep), in NBC it becomes narrower with a drop in oxygen concentrations beginning at a greater depth (200-1000 m) (Hendrickx & Serrano 2010, Papiol et al. 2017). The largest seasonal variation in the location and thickness of the OMZ in the Pacific Ocean occurs at high latitudes (>40° N), although changes in these limits also occur in tropical areas (Gallo & Levin 2016). The dynamic environmental conditions of the SCP support fishes with tropical, temperate and transitional affinities (Gutiérrez-Sánchez et al. 2007, Rodríguez-Romero et al. 2008). A reduced OMZ north of BC (290-954 m) compared to the south (136-1205 m) may relate to changes in salinity and temperature (Papiol et al. 2017) and results in a diversity transitional zone in decapod crustacean assemblages at approximately 26° N.

Most of the limited work on deep-sea fishes in the Mexican Pacific was carried out during voyages of the 'Albatross' (Garman 1899, Towsend & Nichols 1925), with additional information available in isolated records (Castro-Aquirre 1981, Castro-Aquirre & Balart 1996, Castro-Aguirre et al. 2007a, b, González-Acosta et al. 2010) and in work that focused on the hake fishery in the northern Gulf of California (López-Martínez et al. 2012). However, recent 'TALUD' cruises (1989-2014) (described in more detail in 'Materials and methods') provide novel information on the distribution and abundance of demersal fishes in this region (Aguirre-Villaseñor & Castillo-Velázquez 2011, Aguirre-Villaseñor & Salas-Singh 2012, Aguirre-Villaseñor et al. 2013, 2016, Cruz-Acevedo et al. 2017a,b). This work describes assemblages of bathydemersal fishes (300-2100 m) off BC and evaluates their relationship with latitude and environmental factors, and represents an ongoing effort to enhance basic understanding of deep-sea fish communities throughout the Mexican Pacific.

## MATERIALS AND METHODS

## Sampling area

As part of the TALUD project ('talud' means 'slope' in Spanish, as in continental slope), the oceanographic vessel 'El Puma' carried out a total of 3 research cruises off BC (Fig. 1): 1 in the southern part of the region (SBC: TALUD XV, July–August 2012, 23–27° N) and 2 in the northern part (NBC: TALUD XVI, July 2013 and XVI-B, May–June 2014; 28–32° N).

#### Sampling and analysis of environmental factors

In order to find flat bottoms that allowed sampling, the bathymetry and the average depth of each station were explored (Multibeam Kongsberg EM300 echo sounder; 38 kHz, maximum depth: 6000 m). Temperature and DO concentrations were measured approximately 20 m above the bottom, with a CTD-O<sub>2</sub> (Seabird 19 with oxygen probe) and rosette-mounted 10 l Niskin bottles (Papiol et al. 2017). DO concentrations were corroborated using the Winkler titration method (Strickland & Parsons 1972). Forty sediment samples were collected with a modified USNEL box core, with a maximum capacity of 80 l (Hendrickx 2012). From each station, 10 cm of surface sediment were taken and frozen at  $-20^{\circ}$ C. In the laboratory, sediments were dried to a constant weight at 60°C (Papiol et al. 2017). We determined the percentage of organic matter (OM) (El-Rayis 1985) and organic carbon (OC) content in sediments, as indirect measures of food availability (Drazen & Sutton 2017). Samples were treated with an oxidizing mixture of 1N  $K_2Cr_2O_7$  + concentrated  $H_2SO_4$  +  $Ag_2SO_4$ , and then titrated with 0.5 N Fe(NH<sub>4</sub>)<sub>2</sub>(SO<sub>4</sub>)<sub>2</sub> (Loring & Rantala 1992). Solutions of dextrose were used to develop calibration curves. Grain size distribution was determined by laser dispersion (Malvern Mastersizer 2000E) on sediment samples, after treatment with 30%  $H_2O_2$  to destroy organic matter (Papiol et al. 2017).

To conduct exploratory analyses and reduce the number of predictors in relevant analyses, we examined Pearson's correlations among all environmental factors obtained: depth, temperature, DO, latitude, salinity, OM, OC, percentage of clays (Clay), percentage of silt (Silt) and percentage of sand (Sand). For pairs with correlations greater than 0.6, only 1 factor was chosen for use in subsequent analyses (Anderson & Willis 2003, Papiol et al. 2017).

## Sampling of demersal fishes

TALUD provides fishery-independent data on demersal fish biodiversity for the continental slope of the Mexican Pacific. TALUD used a benthic sledge (2.35 m wide, 0.90 m high) equipped with a collecting net of about 5.5 cm stretched mesh size, operated at depths from 304 to 2124 m. The topographic complexity of some sites prevented the use of larger trawl nets (Hendrickx 2012). The net was towed for an average of 30 min at a ship speed of 2 knots. All specimens were separated and fixed with a 4% formaldehyde seawater solution for at least 1 wk, washed with tap water and preserved in 70% ethanol. In the laboratory, the specimens were identified to species level following Nelson (2006). We removed pelagic species from the data set prior to analysis because bottom trawls did not adequately capture these species. Because bathydemersal fish were not caught in all trawls, only 31 samples were included in assemblage analyses. The density of the bathydemersal species were estimated from the number of captured specimens in each station per swept area (ind.  $ha^{-1}$ ).

#### Assemblage structure

We conducted 2 separate cluster analyses (Clarke & Warwick 2001, Murtagh & Legendre 2014) and 1 exploratory non-metric multi-dimensional scaling

ordination (nMDS, Clarke & Warwick 2001) to corroborate the assemblages observed in cluster analyses (Minchin 1987) using the 'vegan' (Oksanen et al. 2016) and 'MASS' packages (Ripley et al. 2016) in the R 3.2.2 software (R Core Team 2016). First, we clustered trawls by species with the aim of understanding spatial patterns in assemblage structure. Second, we clustered species based on trawls (co-occurrence across sites) to determine which species formed assemblages. For each analysis, we used the Bray-Curtis dissimilarity index (Bray & Curtis 1957). Ward's linkage method was chosen to prioritize the formation of homogeneous groups (Hoff & Stevens 2005, Murtagh & Legendre 2014). Data were fourthroot transformed prior to analysis to reduce the influence of highly abundant species (Ter Braak 1986). We used a similarity profile analysis (SIMPROF, p < 0.05) to identify the significant clusters (Primer v6 + PERMANOVA software; Clarke & Warwick 2001).

To determine the main abiotic factors influencing species distribution, we conducted 2 canonical analyses of principal coordinates (CAP, Anderson & Willis 2003). In the first analysis, we included depth, latitude, Clay, OC and salinity as continuous predictors. Environmental variables were normalized prior to analysis. The approach essentially runs a distancebased redundancy analysis (db-RDA) and a principal coordinates analysis (PCoA) for dependent (species densities) and normalized environmental factors. However, since the environmental data are continuous and the model is linear, this approach may not capture non-linear trends in species assemblages such as abundance of a species or species at middepths. Therefore, we conducted a second CAP in which we binned trawls into 5 depth×latitude groups based on the results of the cluster analyses above (see 'Results'): South-Shallow (South-S), South-Medium, (South-M), South-Deep (South-D), North-Medium (North-M) and North-Deep (North-D). This second CAP allowed us to better resolve assemblage structure at mid-depths. Ordinations were performed in R 3.2.2 (R Core Team 2016) using the 'vegan' (Oksanen et al. 2016) and 'MASS' packages (Ripley et al. 2016).

To evaluate the combined effect of latitude and depth on the distribution of species and which assemblages differed from each other, we used a distance-based permutational multivariate analysis of variance (PERMANOVA, Anderson et al. 2008). A 1-factor PERMANOVA design was used to compare 4 of the latitude–depth strata: South-S, South-M, North-M and North-D. We used pairwise tests to identify the pairs of groups that were distinct from each other. The p-values were obtained using 999 permutations, and significance was set at p < 0.05. We used the similarity percentage routine (SIMPER) to identify the most important species in each depth–latitude assemblage in terms on density (Clarke 1993). For these analyses, we used the Primer v6 + PERMANOVA software (Clarke & Warwick 2001).

# Diversity

We examined 3 key components of species diversity: species richness, species density and species evenness (Hurlbert 1971, Heck et al. 1975, Gotelli & Colwell 2001). Because the number of observed species increases with sampling effort (Rosenzweig 1995), we calculated individual-based (standardized to number of species per n individuals) and samplebased (standardized to the number of species per n trawls and here extrapolated to the covered area) species accumulation curves for species richness and species density, respectively. We also conducted individual-based rarefaction to estimate species richness for each trawl for later analyses (see below). We calculated species accumulation curves for 4 of the latitude-depth strata: South-S, South-M, North-M and North-D. Species richness and species density provide different insights about diversity. True richness is the absolute number of species observed in an exhaustive sample of an area, but it is usually presented in its rarefied form as number of species per some number of individuals. Species density is the number of species per specified area (point along the x-axis in the accumulation curve, often some number of samples from sample-based rarefaction or total area sampled) and is more relevant for conservation because it indicates the number of species affected by any spatial management (Worm et al. 2006, Gotelli & Colwell 2011, Tolimieri et al. 2015). We calculated Gini-Simpson diversity index  $(1 - \lambda)$  as a measure of evenness, since it is easily interpreted as the probability that the next individual in the sample will be of a different species than the current one (Hurlbert 1971). This index takes into account the number of species and their relative abundance (Hill 1973). All calculations for richness, density and evenness were performed in R 3.2.2 (R Core Team 2016) using the 'vegan' package (Oksanen et al. 2016).

We used generalized additive models (GAMS, Hastie & Tibshirani 1990) to analyze relationships between uncorrelated habitat variables and both Simpson diversity and rarefied species richness. We included depth, DO, latitude, Clay, OC and salinity in the analyses. We excluded other potential predictors because they were correlated with one of the above variables (see 'Results') except for DO, which was highly correlated with depth but is a determinant factor in vertical distribution of species in regions with strong OMZs (Levin 2003, Gallo & Levin 2016). We chose GAMs to account for potential non-linear relationships in the data and because we could not predict the form of any such relationship *a priori*. All models were fit in R 3.2.2 (R Core Team 2016) using the 'gamlss' package (Rigby & Stasinopoulos 2005).

For evenness (Gini-Simpson index), we used a GAM with a 0-inflated beta-distribution and logitlink since the values were bound between 0 and 1 but included numerous 0s (where only 1 species was present). We used a forward-stepwise procedure using Akaike's information criterion (AIC) to choose the best-fit model from the predictors (Burnham & Anderson 1998). However, since there were only 27 data points, we limited the number of predictors in the final model to 2 to avoid over-fitting. Initial model evaluations used a 'loess' smoother because there were potentially multiple smoothed predictors in the model. However, since the best-fit model included only 1 predictor (DO), we then re-fit the model using a penalized spline (Rigby & Stasinopoulos 2005).

For (rarefied) species richness, we used a GAM with a Gamma distribution and log-link, since the data were continuous and bounded between 0 and positive infinity (the data were rarefied species richness and could thus take fractional values). Since some trawls had few individuals, making rarefaction difficult, we excluded trawls with fewer than 9 individuals, resulting in 16 usable trawls. Because there were only 16 data points, we did not explore models with multiple predictors. Instead we fit each predictor individually and evaluated models versus the null model using AIC to determine whether there was any evidence for a relationship between the habitat variables and species richness. We also evaluated each GAM to determine whether the relationship was linear or non-linear by examining the estimated degrees of freedom.

# RESULTS

# **Species sampling**

TALUD carried out a total of 48 bottom trawls from 2012 to 2014, covering approximately 23.10 ha (TALUD XV = 22, TALUD XVI = 2, TALUD XVI-B = 24; Fig. 1). In total, 3417 fish were caught, belonging to 77 species, 36 families and 18 orders; of these, 27 species were mesopelagic and 10 species were bathypelagic. The remaining 40 species were bathydemersal (Table 1). Fish were caught in all trawls but only 31 of 48 (71%) trawls caught bathydemersal species. These 31 trawls are analyzed here.

#### **Environmental gradients**

Several environmental variables showed strong correlations with each other (r > 0.6): depth-temperature-DO (Fig. 2a,b), OC-OM and Clay-Silt-Sand. Other factors showed weaker correlations and fell below our threshold of r = 0.6 (Table 2, and see Fig. S1 & Table S1 in the Supplement at www.intres.com/articles/suppl/m592p225\_supp.pdf). Salinity was significantly correlated with depth (Fig. 2c), DO, latitude and temperature. Clay was positively correlated with depth, DO, OC and OM, and negatively correlated with temperature. Silt and Sand were correlated with latitude, OC and OM. From these comparisons, depth, latitude, salinity, OC and Clay were selected for the direct analysis of gradients. Three water masses were identified at 20 m above the bottom: NPIW (depth: 578-885 m; 27°9'-32°N), PIW (depth: 554-1008 m; 23°8'-27°12' N), PDW (depth: 1071-2124 m; 23-31°42' N; Fig. 2d).

## Assemblage structure

We first clustered trawls based on species to better understand the spatial structure of assemblages. The resulting tree showed clustering of trawls by latitude (north or south) and depth (Fig. 3a). The first 2 branches separated the deepest trawls from the shallow and medium depth stations. Five significant clusters were obtained (SIMPROF, p < 0.05): (A) upper slope of SBC (South-Shallow, 304-658 m), clustering stations inside the OMZ (0.05–0.15 ml  $l^{-1}$ ); (B) middle slope of SBC (South-Medium, 779–1228 m, 0.12–0.61 ml l<sup>-1</sup>), dominated by Bathypterois atricolor, B. ventralis and Nezumia liolepis; (C) middle slope of NBC (North-Medium, 730-1053 m), grouping trawls inside the OMZ  $(022-0.48 \text{ ml } l^{-1})$ ; (D) lower slope of NBC (North-Deep; 1318, 1396 and 1448 m), dominated by Coryphaenoides acrolepis and located below the OMZ (0.76–0.9 ml  $l^{-1}$ ); (E) northern-southern lower slope (North-Deep, mainly), grouping the deepest and more oxygenated trawls of NBC (1402-2082 m, 0.92-1.83 ml l<sup>-1</sup>) with 1 trawl from SBC (1430 m,

Table 1. Deep-sea fishes caught off the western coast of Baja California during the TALUD project. Sp-ID: species code for ecological analysis; abundance: % of total abundance; min-max: distribution range for each species; +: new latitudinal record. Latitude is given in decimal coordinates

Order, Family	Species	Sp_ID	Habitat	Abun- dance (%)	Latitude (°N) (min-max)	Depth (m) (min-max)	Oxygen (ml l <sup>-1</sup> ) (min-max)
Myxiniformes Myxinidae	Eptatretus stoutii (Lockington, 1878) Myxine circifrons Garman, 1899	Eps Myc	Bathydemersal Bathydemersal	0.20 0.06	26.62–31.77 25.07–29.40	554–986 1228–1448	0.07-0.48 0.44-0.90
Carcharhiniformes Pentanchidae Scyliorhinidae	<i>Cephalurus cephalus</i> (Gilbert, 1892) <i>Parmaturus xaniurus</i> (Gilbert, 1892) <i>Apristurus brunneus</i> (Gilbert, 1892)	Cec Prx Apb	Bathydemersal Bathydemersal Bathydemersal	0.18 0.09 0.06	23.43 27.16 28.8–30.66	658 578 763-774	0.08 0.07 0.22-0.23
Rajiformes Rajidae	<i>Raja</i> sp.	Ra1	Bathydemersal	0.03	24.55	1224	0.65
Anguiliformes Congridae Nemichthyidae	Bathycongrus varidens (Garman, 1899) Avocettina bowersii (Garman, 1899) Nemichthys scolopaceus Richardson, 1848 Facciolella equatorialis (Gilbert, 1891)	Btv Avb Nms Fae	Bathydemersal Bathypelagic Mesopelagic Bathypelagic	0.03 0.18 0.35 0.64	24.33 23.3-30.82 23.01-30.66 27.16-29.35	304 304 1409–2056 730–2046 578–730	0.05 0.9-1.43 0.23-1.83 0.07-0.28
Serrivomeridae	venenca tenacuata Cannan, 1099 Serrivomer sector Garman, 1899	Srs	Bathypelagic	0.06	23.01-29.14	1104-1430	0.40-0.61
Halosauridae Sacconharvnoiformes	Halosaurus attenuatus Garman, 1899	Haa	Bathydemersal	0.03	23.3	1430	06.0
Cyematidae Alenorenhaliformes	<i>Cyema atrum</i> Günther, 1878	Cmy	Bathypelagic	0.03	28.47	2046	1.83
Alepocephalidae	Alepocephalus tenebrosus Gilbert, 1892 Talismania bifurcata (Parr, 1951)	Alt Tab	Bathydemersal Bathydemersal	0.35 0.03	23.21–30.66 29.35	730-1134 730	0.23 - 0.50 0.28
Usmeruormes Bathylagidae Diatthroctidae	Bathylagus pacificus Gilbert, 1890 Leuroglossus stilbius Gilbert, 1890 Distrituccidae con	Bhp Lus D1	Mesopelagic Mesopelagic	0.29 1.35 0.02	26.4 - 31.08 23.01 - 29.91 30.63	754-2124 534-1854 1400	0.25-1.62 0.06-1.52 0.00
rtaugu ocudae Stomiiformes	rialy locutude sp.	111	INTEROPETADIC	c0.0	00.00	1403	0.90
Gonostomatidae	<i>Cyclothone acclinidens</i> Garman, 1899 <i>Cyclothone signata</i> Garman, 1899	Cya Cys	Mesopelagic Mesopelagic	$6.50 \\ 0.15$	23.21 - 31.71 28.78 - 29.35	763-2124 1261-1854	0.12 - 1.73 0.76 - 1.52
Ipnopidae + +	<ul> <li>Bathypterois atricolor Alcock, 1896</li> <li>Bathypterois ventralis Garman, 1899</li> </ul>	Baa Bav	Bathydemersal Bathydemersal	0.88 1.52	23.21 - 30.85 23.01 - 27.20	1008–2083 779–1228	0.22 - 1.47 0.11 - 0.65
Phosichthyidae Sternoptychidae	Vinciguerria lucetia (Garman, 1899) Argyropelecus affinis Garman, 1899 Argyropelecus luchnus Garman, 1800	Vil Ara Arl	Mesopelagic Mesopelagic Mesopelagic	0.26 0.76 0.59	23.38 25.44-31.77 24 33-31 77	1008 754-2056 304-2124	0.22 0.23 - 1.43 0.05 - 1.62
Stomiidae	sugyroperectus systumes commen, 1039 Sternoptyx obscura Garman, 1899 Stomias atriventer Garman, 1899 Stomidae sp.	Sno Sta St1	Mesopelagic Mesopelagic Bathypelagic	0.03 0.03 0.03 0.03	24.00-01.77 29.86 23.01-31.80 30.93	304-2124 1393 730-2124 1318	$0.03^{-1.02}$ 0.97 $0.12^{-1.62}$ 0.76
Aulopiformes Paralepididae Scopelarchidae	Lestidium sp. Scopelarchoides nicholsi Parr, 1929	Le1 Son	Mesopelagic Mesopelagic	0.03 0.09	28.67 23.21–31.37	1403 1134 - 1497	0.92 0.50–0.93
Myctophidae	Stenobrachius leucopsarus	Sbl	Mesopelagic	0.06	26.97-26.97	1444	1.02 - 1.02
	(Eugenmenn & Eugenmann, 1090) Triphoturus mexicanus (Gilbert, 1890) Triphoturus nigrescens (Brauer, 1904)	Trm Trn	Mesopelagic Mesopelagic	5.82 0.32	23.21 - 31.77 23.01 - 31.71	730-2124 1053-2124	0.12 - 1.62 0.40 - 1.62

Neoscopelidae	Scopelengys tristis Alcock, 1890 Scopeloberyx sp. Scopeloaadus mizolenis bispinosus (Gilbert, 1915	Sct Sc1 Scb	Mesopelagic Mesopelagic Mesopelagic	0.09 0.56 0.06	25.25-29.91 23.01-30.66 23.3-28.78	754-1790 763-2124 1261-1430	0.25-1.07 0.22-1.62 0.76-0.90	
Gadiformes Macrouridae ++	Coryphaenoides acrolepis (Bean, 1884) Coryphaenoides anguliceps (Garman, 1899) Coryphaenoides capito (Garman, 1899) Nerrumia convergens (Garman, 1899)	Coa Coa Nec	Bathydemersal Bathydemersal Bathydemersal Bathydemersal Bathydemersal	0.18 0.26 0.15 0.03	29.4-31.71 29.4-31.71 23.21-30.82 23.43-26.62 23.43-26.62 23.67 23.01	1318–1448 1134–2056 554–658 1403 534–1738	0.76-0.90 0.50-1.83 0.08-0.15 0.92 0.96	
Merlucciidae Moridae	Nezuma notepis (cnoett, 1090) Nezumia stelgidolepis (Gilbert, 1890) Merluccius productus (Ayres, 1855) Antimora microlepis Bean, 1890 Laemonema verecundum (Jordan & Cramer, 1897 Physiculus rastrelificer Gilbert, 1890	Nes Nes Anm 7)Lav Phr	Bathydemersa Bathydemersal Mesopelagic Bathydemersal Bathypelagic Bathydemersal	30.11 3.96 0.85 0.06 0.15 0.06	26.62–28.80 26.62–28.80 24.33–27.16 29.35–30.83 29.33 27.16 27.16	554-774 554-774 304-578 1520-1854 304 578	0.00-0.00 0.15-0.22 0.05-0.07 0.96-1.52 0.05 0.07	
Ophidiiformes Bythitidae Ophidiidae	<i>Cataetyx rubrirostris</i> Gilbert, 1890 <i>Cherublemma emmelas</i> (Gilbert, 1890) <i>Dicrolene filamentosa</i> Garman, 1899 Ophidiidae sp.	Car Che Dif Op1	Bathydemersal Bathydemersal Bathydemersal Bathypelagic	0.50 31.28 0.12 0.03	28.8–30.66 23.41–27.16 23.21–23.38 23.14	730–2028 304–800 1008–1134 951	0.22-1.60 0.05-0.15 0.22-0.50 0.29	
Lophiiformes Ogcocephalidae -+ Oneirodidae	Dibranchus spinosus (Garman, 1899) - Dibranchus spongiosa (Gilbert, 1890) Oneirodidae sp. 1 Oneirodidae sn. 2	Dip Dis On 1	Bathydemersal Bathydemersal Mesopelagic Mesomelagic	0.06 2.46 0.03 0.03	$\begin{array}{c} 23.38\\ 23.41{-}26.62\\ 23.59\\ 23.59\\ 23.59\end{array}$	1008 554–800 616 616	0.22 0.08-0.15 0.01	
Stephanoberyciformes Melamphaidae	Poromitra crassiceps (Günther, 1878) Poromitra sp.	Poc Po1	Mesopelagic Mesopelagic	0.20	24.45-29.28 25.07-30.63	774–2124 1228–2046	0.22-1.83 0.44-1.83	
Cetomimitormes Cetomimidae Scorpaeniformes Liparidae	Cetomimidae sp. Paraliparis sp. 1 Paraliparis sp. 2	Ct1 Pa1 Pa2	Mesopelagic Bathydemersal Bathydemersal	0.03 0.03 0.03	28.47 24.55 23.41	2046 1224 800	1.83 0.65 0.11	
Perciformes Chiasmodontidae	<i>Paraliparis</i> sp. 3 Liparidae sp. <i>Chiasmodon</i> sp.	Pa3 Ps1 Ci1	Bathydemersal Bathypelagic Mesopelagic	0.03 0.06 0.06	27.20 24.55–29.86 26.42–29.28	7791224 $-1393$ 1516 $-1689$	0.12 0.65-0.97 0.95-1.26	
Sebastidae Zoarcidae	Chiasmodon subniger Garman, 1899 Sebastolobus altivelis Gilbert, 1896 Bothrocara brunneum (Bean, 1890) Lycenchelys cf. cicatrifer	Ciu Sea Bob Lyi Lyi	Mesopelagic Bathydemersal Bathydemersal Bathydemersal Bathydemersal	0.03 3.28 0.06 0.03 0.03	24.45 28.8–31.77 27.2–31.77 29.35 30.85	$\begin{array}{c} 2107\\ 730-1409\\ 779-986\\ 1854\\ 2083\\ \end{array}$	$\begin{array}{c} 1.73\\ 0.22-0.9\\ 0.12-0.48\\ 1.52\\ 1.47\\ 1.47\\ \end{array}$	
Ŧ	Lycencnerys crotaunus (Gulbert, 1890) - Lycencherys porifer (Gilbert, 1890) Lycencherys sp. 1 Lycencherys sp. 2 Lycodapus dermatinus Gilbert, 1896 Lycodapus fierasfer Gilbert, 1890 Melanostigma pammelas Gilbert, 1896	Lyc Lyp Lyd Lyf Mlp	Bathydemersal Bathydemersal Bathydemersal Bathydemersal Bathypelagic Bathypelagic	0.12 0.03 0.06 0.03 0.32 0.03	28.8-29.91 27.20 27.16 27.16 23.41-31.77 29.4-31.77 28.78	730-774 779 578-1008 578-1053 578-1053 754-1448 754-1448 1261	0.22-0.28 0.12 0.07-0.22 0.07 0.07-0.48 0.25-0.97 0.76	
Pleuronectiformes Bothidae Pleuronectidae	Monolene asaedai Clark, 1936 Microstomus pacificus (Lockington, 1879)	Moa Mip	Bathydemersal Bathydemersal	$0.06 \\ 0.47$	24.33 27.16–29.35	304 578–1053	0.05 0.07-0.40	



Fig. 2. Distribution of (a) dissolved oxygen, (b) temperature, and (c) salinity, measured at 20 m from the bottom, with respect to the depth gradient; (d) temperature-salinity data pairs for all sampling stations. NPIW: North Pacific Intermediate Water; PIW: Pacific Intermediate Water; PDW: Pacific Deep Water

0.9 ml  $l^{-1}$ ). Three intermediate-deep trawls from SBC were not assigned to any cluster by the SIM-PROF test: 1008, 1134 and 1224 m. However, these trawls contained species of the genus *Bathypterois*, similar to the 'B' branch. One deeper trawl from NBC (1409 m) was not significantly related to any cluster but contained a single specimen of *Sebastolobus altivelis*, a species mainly located in stations

from the 'C' branch. When clustering species, we found an effect of latitude, since only 10 species were found both in the southern and northern zones, but depth was not as clearly resolved, mainly because some species of the upper and middle slope were mixed in the clusters (Fig. 3b). The nMDS ordination had low stress (0.04) and agreed with the cluster analysis on the conformation of the lati-

Table 2. Pearson's correlations between all environmental factors obtained off the western coast of Baja California during the TALUD project. \*significant correlations (p < 0.05); \*\*strong correlations (r > 0.6). DO: dissolved oxygen, OC: organic carbon, OM: organic matter

Pearson	Temperature	DO	Latitude	Salinity	OC	OM	Clay	Silt	Sand
(r)	(°C)	(ml l <sup>-1</sup> )	(°N)		(%)	(%)	(%)	(%)	(%)
Depth (m) Temperature DO Latitude Salinity OC OM Clay Silt	-0.89**	0.97** -0.82**	0.23 -0.27 0.25	0.57* -0.34* 0.59* -0.45*	-0.16 0.17 -0.15 -0.14 -0.04	-0.16 0.17 -0.15 -0.14 -0.04 1.00**	0.41* -0.32* 0.39* 0.14 0.20 0.48* 0.48*	0.24 -0.15 0.25 0.41* 0.03 0.50* 0.50* 0.64**	-0.28 0.18 -0.29 -0.38* -0.06 -0.52* -0.52* -0.73** -0.99**



Fig. 3. Abundances of bathydemersal fishes, based on a Bray-Curtis resemblance matrix using Ward's method: (a) by depth (m) and (b) by species. A: South-Shallow; B: South-Medium; C: North-Medium; D and E: North-Deep; S: South; N: North. Species codes as in Table 1

tude–depth assemblages. Axis 1 separated the shallow, middle and deep trawls from both southern and northern zones, whereas Axis 2 separated the middle trawls of both zones (Fig. S2). The results of the ordination and classification procedures showed 5 assemblages: South-S ( $<28^{\circ}$ N, 300–700 m, 15 species), South-M ( $<28^{\circ}$ N, 700–1300 m, 20 species), South-D ( $<28^{\circ}$ N, 1430 m; 1 trawl, 4 species), North-M ( $>28^{\circ}$ N, 700–1300 m, 12 species) and North-D ( $>28^{\circ}$ N, 1300–2100 m, 10 species).

The CAP (db-RDA) ordination showed a clear latitudinal distribution for species assemblage structure (Fig. 4a), with most stations in the positive quadrant on the *y*-axis (CAP2) belonging to NBC. Variation in assemblage structure by depth was less distinct but present, seen primarily between North-M and North-D, but with overlap in South-S and South-M. This lack of clear depth segregation is due to a non-linear relationship between depth and assemblage structure (see below). The first 2 CAP axes explained 74.2% (CAP1: 47%, CAP2: 27.2%) of the variance in assemblage structure. CAP1 was positively correlated to depth (r = 0.89) and salinity (r = 0.79), whereas CAP2 was positively correlated to latitude (r = 0.93, p < 0.01) and Clay (r = 0.38, p = 0.03), and negatively correlated to salinity (r = -0.41, p < 0.01). The

CAP 1 Fig. 4. Canonical analysis of principal coordinates (CAP) for bathydemersal fishes with respect to environmental factors: (a) based on distance-based redundancy analysis (db-RDA), and (b) a categorical version based on discriminant analysis. Only species with significant correlations (r > 0.35, p < 0.05) are shown. Clay: % clay in sediments; Lat: Latitude; OC: % organic carbon in sediments; Salt: salinity; Alt: *Alepocephalus tenebrosus*; Baa: *Bathypterois atricolor*; Bav: *Bathypterois ventralis*; Che: *Cherublemma emmelas*; Lyd: *Lycodapus dermatinus*; Nel: *Nezumia liolepis*; Sea: *Sebastolobus altivelis* 

species ordination in the CAP1 was negatively correlated with *Cherublemma emmelas* (r = -0.47, p < 0.01), *Lycodapus dermatinus* (r = -0.55, p < 0.01), *N. liolepis* (r = -0.99, p < 0.01), *Nezumia stelgidolepis* (r = -0.41, p < 0.01) and *S. altivelis* (r = -0.67, p < 0.01). Except for *C. emmelas* and *N. stelgidolepis*, all of these species are from medium depths (800–1000 m). The CAP2 ordination was mainly affected by the latitude. CAP2 was negatively correlated with *B. atricolor* (r = -0.44, p < 0.01), *B. ventralis* (r = -0.85, p < 0.01) and *C. emmelas* (r = -0.36, p = 0.03) from the South-S and South-M depth sites, and positively correlated with *S. altivelis* (r = 0.64, p < 0.01) from the North-S and North-M depth sites.

The categorical CAP (discriminant-type analysis) (Fig. 4b) distinguished the intermediate depths from the south and north assemblages, showing a clear depth-latitude relationship. The first 2 CAP axes explained 75.8% of the variance in assemblage structure (CAP1: 47.5%, CAP2: 28.3%). Bathypterois ventralis was related to the South-M cluster, whereas *L. dermatinus*, *N. liolepis*, *Alocephalus tenebrosus* and *S. altivelis* were related to both North-M and South-M clusters.

There were significant differences in the assemblage structure among these 4 latitude-depth strata (PERMANOVA, pseudo- $F_{3,23} = 5.8$ , p < 0.01). All strata evaluated differed significantly (post hoc comparisons, Table 3). Cherublemma emmelas, N. liolepis, Dibranchus spongiosa and Coryphaenoides capito provided 91% (Table 4) of the structure for South-S (SIMPER, average similarity: 34.41%); the first 2 species also had the greatest abundances in all samples (Table 1). South-M (average similarity: 41.56%) was dominated by 2 species widely distributed throughout the ECP: B. ventralis and N. liolepis (92.16% of the accumulated contribution). South-D was not evaluated because it contained only 1 trawl in which 3 individuals were caught (B. atricolor, Halosaurus attenuatus and Venefica tentaculata). North-M had the highest average similarity (62.26%), North-D had the lowest average similarity (13.75%) and was mainly structured by C. anguliceps and C. acrolepis. High dissimilarities were observed in the distribution of species among all assemblages (84-100%, Table 3). South-M and

North-M were the most similar assemblages to each other (22.02%), because in both assemblages, *N. liolepis* had an important contribution to their species conformation.

#### Diversity

The species accumulation curves (rarefied by trawl or number of specimens) showed a declining number of additional species with additional sampling effort,



Table 3. Results of PERMANOVA pairwise comparisons for the latitude–depth assemblages of bathydemersal fishes caught off the western coast of Baja California during the TALUD project. S: shallow, M: medium, D: deep

Comparisons	t	p (perm)	Average dissimilarity (%)
South-S vs. South-M	2.41	0.002	86.61
South-S vs. North-M	2.99	0.005	83.08
South-S vs. North-D	1.92	0.002	100.00
South-M vs. North-M	3.11	0.001	77.98
South-M vs. North-D	2.31	0.002	96.36
North-M vs. North-D	2.60	0.001	97.32

but did not appear to approach an asymptote (Fig. 5a,b; 40 species and 2644 specimens in 31 trawls). Thus, substantially more sampling effort is necessary to better sample the community in terms of estimating true species richness.

Species density (species per specified area) was higher in the south than in the north (compare the curves in Fig. 5c for 5 trawls), although there was considerable uncertainty in some estimates. North-D likely had the lowest species density, with North-M

Table 4. Latitude–depth assemblages obtained by SIMPER analysis carried out for bathydemersal fishes caught off the western coast of Baja California during the TALUD project. Cut-off at cumulative contributions of 90 %

Assemblage	Average abundance	Average similarity	Cumulative contribution (%)
South-Shallow			
Average similarity: 34.41 %	)		
Cherublemma emmelas	0.38	27.22	64.43
Nezumia liolepis	0.18	4.93	78.76
Dibranchus spongiosa	0.14	2.23	85.25
Coryphaenoides capito	0.08	2.02	91.12
<b>South–Medium</b> Average similarity: 41.56 % <i>Bathypterois ventralis</i> <i>Nezumia liolepis</i>	0.19 0.19	20.86 17.44	50.20 92.16
<b>North–Medium</b> Average similarity: 62.26 %	)		
Nezumia liolepis	0.27	18.84	30.26
Sebastolobus altivelis	0.25	18.74	60.37
Lycodapus dermatinus	0.16	11.52	78.87
Alepocephalus tenebrosus	0.10	4.58	86.23
Eptatretus stoutti	0.07	2.19	89.75
Cataetyx rubrirostris	0.09	2.19	93.27
North–Deep Average similarity: 13.75%	, , , , , , , , , , , , , , , , , , ,	8.05	58 51
Coryphaenoides acrolepis	0.04	4.63	92.21

being slightly lower than but more similar to the southern zones.

Species richness was higher in South-M than the other zones (compare the curves in Fig. 5d at 200 individuals) and increased rapidly with increased sampling, with no evidence of approaching an asymptote. North-M appeared to have intermediate species richness. North-D was difficult to compare with the other zones due to the lower overall abundance of individuals. While South-S had slightly lower richness than North-M when compared at 400 individuals, both appeared to show similar asymptotes at higher sampling and may have similar richness.

Evenness (Gini-Simpson index,  $1 - \lambda$ ) varied with depth and latitude. North-D had the highest evenness  $(1 - \lambda = 0.82; 10 \text{ species and } 20 \text{ individuals in } 11 \text{ trawls})$ . Evenness was intermediate in the South-M (0.67; 20 species and 208 individuals in 8 trawls) and North-M assemblages (0.68; 12 species and 418 individuals in 6 trawls). South-S had the lowest evenness (0.57; 15 species and 1994 individuals in 5 trawls), where *C. emmelas* and *N. liolepis* were the dominant species. Thus overall, South-M was the most diverse

area, with high species density and the highest species richness and the second highest evenness.

# Species richness, evenness and environmental predictors

Among the univariate models tested, DO (AIC = 31.13) and depth (AIC = 32.16) were the best predictors of species richness and were essentially equivalent, varying by just over 1 AIC point. Richness increased with both DO and depth. For DO, richness was lower around 0.1–0.2 ml l<sup>-1</sup>, maintaining similar values within the OMZ and increased in the oxygenated zone. However, this increase at high DO should be interpreted cautiously since it is driven by only 1 point (Fig. 6a). Given that DO is more likely to directly affect physiology, the depth-richness relationship is likely a proxy for the DO effect. The richness-DO relationship was non-linear (effective degrees of freedom, edf = 2.00) as was the relationship with depth (edf = 2.00). Of the other predictors, none (Fig. 6b) was better than the null model (AIC = 41.08): latitude (AIC = 42.54), OM (AIC = 42.64), salinity (AIC = 42.68) and Clay (AIC = 42.72).



Fig. 5. Rarefied species accumulation curves for bathydemersal fishes, based on (a) species density by trawls, (b) species richness, (c) species density by latitude–depth strata, (d) species richness by latitude–depth strata. Vertical bars: standard deviation

For Gini-Simpson diversity, the best-fit model included only salinity (Fig. 7a) as a predictor (AIC = 2.06) and differed from the null model by almost 10 AIC points (AIC = 11.61). Among the other predictors, depth (AIC = 8.54) and DO (AIC = 10.16) (Fig. 7b,c) fit better than the null model. However, OM ( $\Delta AIC = 12.79$ ), Clay ( $\Delta AIC = 15.64$ ) and latitude ( $\Delta AIC = 15.92$ ) did not. Adding terms to the salinity model did not increase model fit. The best 2-factor model, salinity–OM (AIC = 2.82), was worse than the single-factor salinity model. The Gini-Simpson index showed a non-linear relationship to salinity, as 2 maximum peaks were observed; the first peak was located between 34.40 and 34.45 salinity, whereas the second one was around the value of 34.60. The lowest values of Gini-Simpson were located mainly between 34.50 and 34.56 salinity (Fig. 7a). Gini-Simpson values increased as OD concentrations increased within OMZ (<0.5 ml  $l^{-1}$ , 200–1300 m), but this trend was not maintained in the oxygenated zone (>0.5 ml  $l^{-1}$ , >1300 m; Fig. 7b,c).

# DISCUSSION

#### **Oceanographic context**

The main regional oceanographic conditions were similar between the different cruises, making the results comparable among years. The 3 cruises studied here were conducted during the summer (May–August) when the supply of temperate waters

from the Northeastern Pacific is minimal, and for 3 consecutive years during which El Niño–Southern Oscillation had a similar influence on the study area (average Oceanic Niño Index = 2012:  $-0.13 \pm 0.34$ , 2013:  $-0.28 \pm 0.07$ , 2014:  $-0.02 \pm 0.37$ ; NOAA 2017).



Fig. 6. Rarefied species richness for bathydemersal fishes, as a function of (a) concentration of dissolved oxygen and (b) depth. Points: original data; solid lines: back-transformed GAM functions; dashed lines: SE



Fig. 7. Gini-Simpson diversity index for bathydemersal fishes, as a function of (a) salinity, (b) concentration of dissolved oxygen and (c) depth. Points: raw Gini-Simpson diversity; solid lines: back-transformed GAM functions for the mean; dashed lines: SE

A latitudinal shift was observed in DO concentrations (SBC OMZ: 50-1200 m; NBC OMZ: 200-1000 m) and salinity (NBC average salinity: 34.31; SBC average salinity: 34.53), showing the influence of different water masses in the upper and middle slope (~200-1000 m; NPIW in NBC, ESsW and PIW in SBC) (Papiol et al. 2017, this study). SBC had a layer of extreme hypoxia (<0.2 ml l<sup>-1</sup>; Helly & Levin 2004) between 304-800 m, being a possible physiological barrier for some species (Table S1 in the Supplement). The limits and thickness of the OMZ in BC were similar to those previously recorded in SCP (Levin 2003, Watling et al. 2013, Gallo & Levin 2016) and only as broad as the OMZ recorded in the Arabian Sea (~150–1000 m); these 2 regions contain the major OMZs in the world (Levin 2003, Banse et al. 2014, Gallo & Levin 2016). The combined effect between latitude, strong OMZs, water masses and depth has been clearly observed in deep-sea assemblages (Hamukuaya et al. 2001, Clark et al. 2010, Anderson et al. 2013, Papiol et al. 2017, Quattrini et al. 2017), so these relationships were explored in this work and are discussed below.

## Assemblage structure

The depth assemblages described here were similar to those observed in crustaceans (Hendrickx & Serrano 2010, Papiol et al. 2017), mollusks (Zamorano et al. 2007) and polychaetes (Méndez 2007) within the Mexican Pacific slope, which were affected by DO concentrations and water masses. The shallowest assemblages in the OMZ had the most dominant species (Table 1): Cherublemma emmelas and Nezumia liolepis are widely distributed in the ECP (Fischer et al. 1995, Aguirre-Villaseñor & Castillo-Velázquez 2011), whereas N. liolepis and Sebastolobus altivelis are common in SCP (Cross 1987, Hoff et al. 2000, Jacobson et al. 2001). The lower limit of the middle strata was not clearly identified, due to the combined effect of latitude, depth and the OMZ on the distribution of the species. The deeper limit of the OMZ and the distribution limits of some species (Alepocephalus tenebrosus, Bathypterois ventralis, Bothrocara brunneum, Dicrolene filamentosa, Eptatretus stoutii, Lycodapus dermatinus, Microstomus pacificus and N. liolepis) are located within this depth zone, converging with species that were recorded inside and outside of the OMZ (Lycodapus fierasfer, S. altivelis, Cataetyx rubrirostris and Bathypterois atricolor). DO tends to recover at depths greater than ~1000 m, due to the contribution of intermediate and deep water masses (De La Lanza-Espino 1991, Papiol et al. 2017). The latitudinal assemblages observed here are affected by the confluence of tropical and temperate water masses, as are those described for decapod crustaceans from the same cruises as ours (865-2165 m depth; Papiol et al. 2017) and for demersal fishes from the continental shelf and the upper slope of BC (30-500 m depth; Rodríguez-Romero et al. 2008, Green-Nieto 2011).

The upper and middle slope assemblages of SBC contain many widely distributed species from the

Shelf (m)	Upper slope (m)	Middle slope (m)	Lower slope (m)	Region	Reference
50-350	350-600	_	-	Southeastern Atlantic off Namibia	Hamukuaya et al. (2001)
188–216	315-785	686-1369	1533–3075	Northern Gulf of Mexico	Powell et al. (2003)
<200	200-600	Mid-slope: 600–800, Deep mid-slope: 800–1200	-	Mid-Atlantic off the Azores Archipelago	Menezes et al. (2006)
_	<800	800-1200/1300	>1300	Seamounts from the Northeast Atlantic	Menezes et al. (2009)
<200	500	1000	_	Indian Ocean off southern Australia	Currie et al. (2012)
_	Shelf and upper slope: 50–500	700–1200	_	Southwestern Pacific off north-eastern New Zealand	Zintzen et al. (2012)
<150	Shelf break/ upper slope: 150–350, upper slope: 300–600	>600	_	Northeast Atlantic, off the Cape Verde archipelago	Menezes et al. (2015)
-	300-600	600-900	900-1400	Northeastern Pacific off Vancouver Island	De Leo et al. (2017)

Table 5. Vertical deep-sea fish assemblages from some ocean basins

ECP (e.g. B. atricolor, B. ventralis, C. emmelas, Dibranchus spongiosa and N. liolepis; Fischer et al. 1995, Cruz-Acevedo et al. 2017a,b) and appear to be influenced by tropical water masses (ESsW and PIW; Pantoja et al. 2012, Papiol et al. 2017). In NBC, assemblage structure was influenced by temperate water (NPIW; Papiol et al. 2017), and several species recorded there (Antimora microlepis, Coryphaenoides acrolepis, C. rubirostris, L. dermatinus, M. pacificus and S. altivelis) are related to the continental slope of Central and Southern California (Cross 1987, Tolimieri 2007). However, tropical species were also recorded in middle and lower slopes of NBC (e.g. B. atricolor, Coryphaenoides anguliceps and N. liolepis). Thus, NBC can be considered a part of the proposed environmental and faunal transition zone for the SCP ecoregion (Rodríguez-Romero et al. 2008, Wilkinson et al. 2009, Tolimieri & Anderson 2010, Anderson et al. 2013). The lower slope (>2000 m) is a poorly explored area in the eastern Pacific off Mexico (Hendrickx 2012, Cunha et al. 2017).

On a global scale, the confluence of different water masses influences the formation of the demersal fish assemblages of several ocean basins (Table 5). Strong OMZs also influence assemblages from the Southeastern Atlantic off Namibia (Hamukuaya et al. 2001) and the Northeastern Pacific off Vancouver Island (De Leo et al. 2017). These examples show an almost constant vertical zonation on the slope of several ocean basins, agreeing with the results of this study. However, vertical assemblages are not homogeneous in all deep-sea environments, since regional topography, oceanographic processes and water masses can determine assemblages with different vertical limits (D'Onghia et al. 2004, Ross et al. 2015, Quattrini et al. 2017).

## **Species diversity**

This is the first systematic sampling at depths below 500 m in BC, so there are no comparative studies on the possible number of species distributed in deeper environments (>500 m). We provided 8 new records for bathydemersal fish species (Table 1): the extension of the northern distribution for 3 grenadiers (Macrouridae: *C. anguliceps, C. capito* and *Nezumia convergens*), for 2 tripod fish (Ipnopidae: *B. atricolor* and *B. ventralis*; Cruz-Acevedo et al. 2017a) and 1 batfish (Ogcocephalidae: *D. spongiosa*; Cruz-Acevedo et al. 2017b), whereas *B. brunneum* extended its southern limit of distribution, and the first record of *Lycenchelys porifer* out of the Gulf of California was reported. These findings could be related to the latitudinal transition discussed above.

We caught fewer species (n = 40) than had previously been recorded in the continental slope of Southern California (54–56 species), the best-studied area in the SCP (Cross 1987, Tolimieri & Levin 2006, Tolimieri 2007). Studies of BC demersal ecosystems have focused on the continental shelf and the upper continental slope (0–500 m), recording at least 220 species (Balart et al. 2002, Rodríguez-Romero et al. 2008). The rarefaction curves did not reach an asymptote, suggesting that true species diversity is higher than that which we observed (Powell et al. 2003).

We observed a decrease in abundance and number of species in the deepest hauls. This trend has been related to a decrease in food availability (estimated here as OC) in vertical gradients of deep-sea environments (Drazen & Sutton 2017), but OC did not correlate with the distribution of the species. In predominantly soft-sediment environments, the substratum provides food resources for benthic species (Tolimieri et al. 2015). However, the sediment composition was not related to assemblage structure.

As DO increases, species richness and evenness also increase (Tolimieri 2007, Papiol et al. 2017), but the effect of the OMZ on species diversity and biomass is regionally variable (Gallo & Levin 2016, De Leo et al. 2017). South-M was the most diverse stratum. Similarly, off Vancouver Island (De Leo et al. 2017) species richness was higher at middle depths (754 m) and in hypoxic areas (<1.4 ml  $l^{-1}$ ), rather than under severe hypoxia ( $< 0.5 \text{ ml } l^{-1}$ ). South-S was the least diverse stratum, clearly dominated by C. emmelas and N. liolepis. Environments with strong OMZs tend to have low richness and are highly dominated by a few species (Levin 2003), similar to that observed in the biomass of Merluccius capensis, Trachurus t. capensis and Sufflogobius bibarbatus in the shelf assemblages (50-350 m) off Namibia (Hamukuaya et al. 2001), in several species of the genus Sebastolobus in the Northeastern Pacific (De Leo et al. 2017) and in the California margin, where S. altivelis, S. alascanus, M. pacificus and Anaplopoma fimbria are commercially exploited due in part to their high abundances (Jacobson et al. 2001, Levin 2003 and references therein, Tolimieri 2007). These species tolerate low DO and are able to access the resources that are there (Levin 2003). On the other hand, when waters are well mixed along the water column, similar values of diversity and biomass can be observed between the continental shelf and the middle slope, similar to the deep-sea assemblages from off South Australia, where Subantarctic Mode Water around 450-500 m promoted a vertical mix of DO (Currie et al. 2012).

Sampling was carried out in flat and soft bottoms because it is difficult to trawl rough or inclined surfaces with the benthic sledge. It is necessary to explore environments that are not sampled adequately with bottom nets, such as highly sloped areas or those located around submarine canyons that are often regions with high diversity (De Leo et al. 2010, 2017, Tolimieri et al. 2015). To solve this problem, it is necessary to increase the number of bottom trawls, include video recordings using remotely operated vehicles (Hoff & Stevens 2005, King et al. 2006) and sample with depth long-lines, in order to increase the catch of larger species, since they are able to avoid some trawl nets because of their greater mobility (Cross 1987, Fossen et al. 2008).

#### **Zoogeographical considerations**

SCP is an environmental and faunal transition ecoregion (Wilkinson et al. 2009), denoted by the conformation of the demersal assemblages of the continental shelf and the continental slope of Southern California (Tolimieri 2007, Tolimieri & Anderson 2010, Anderson et al. 2013) and the continental shelf and upper slope demersal assemblages of BC (Balart et al. 2002, Rodríguez-Romero et al. 2008, Green-Nieto 2011). Although the present work is based on a relatively small number of trawls and we did not sample at different times of the year, the latitudinal transition in the conformation of species was defined around 28°N. South of this latitude the species predominance was tropical, at least during the summer. In order to define if this transition zone is stable or seasonal, it would be necessary to compare the conformation of the depth assemblages along the SCP during the distinct seasons of the year, increasing the sampling effort in BC by trawling more than once in sites previously visited and during years where the effect of the El Niño-Southern Oscillation is stronger.

Our work provides enough evidence to recognize a latitude-depth zonation in bathydemersal fish assemblages of BC, supported by the observed relationship between environmental trends and species distribution. However, it is important to consider that the area covered by the benthic sledge is smaller than that of the nets used in studies from adjacent regions (Cross 1987, Tolimieri 2007), so it is possible that the sledge did not catch all potential species or their real abundance. Because of this, comparison between BC assemblages and other studies should take into account these limitations (Bergstad et al. 2008, Hendrickx 2012).

#### Conclusions

Our main findings agreed with the general hypothesis that slope fish assemblages are usually found in discrete vertical ranges determined by the depth and the environmental factors associated with it (Levin 2003, Powell et al. 2003 and references therein, Tolimieri & Levin 2006, Anderson et al. 2013). The upper slope was dominated by a reduced number of species, the middle slope was the most diverse stratum, and the lower slope was characterized generally by fewer individuals.

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